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Clades within the ‘higher land birds’, evaluated by nuclear DNA sequences

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Abstract

In this study we investigated the phylogenetic relationships within the ‘higher land birds’ by parsimony analysis of nucleotide DNA sequences obtained from the two nuclear, protein-coding genes, *c-myc* and RAG-1. Nuclear genes have not previously been used to address this phylogenetic question. The results include high jackknife support for a monophyletic Apodiformes (including the Trochilidae). This arrangement was further supported by the observation of an insertion of four amino acids in the *c-myc* gene in all apodiform taxa. Monophyly was also inferred for each of the two piciform groups Galbulae and Pici. Within Pici, the Capitonidae was found to be paraphyletic, with the New World barbets more closely related to the Ramphastidae than to the Old World barbets. Another clade with high jackknife support consists of the Upupidae, Phoeniculidae and Bucerotidae. The families Momotidae and Todidae, and Coraciidae and Brachypteraciidae, respectively, also form well supported monophyletic clades. The results are inconclusive regarding the monophyly of the orders Coraciiformes and Piciformes, respectively.

Key words: Aves – ‘higher land birds’ – Apodiformes – Caprimulgiformes – Coliiformes – Coraciiformes – Trogoniformes – Piciformes – Passeriformes – phylogeny – parsimony – DNA sequences – nuclear genes – *c-myc* – RAG-1

Introduction

The traditional basal division of the class Aves into a paleognathous and a neognathous clade has recently received additional support by analyses of DNA sequence data (Groth and Barrowclough 1999; van Tuinen et al. 2000). These analyses also suggest that the orders Galliformes and Anseriformes (Galloanserae) is the sister-group to all other neognathous birds. This latter group, containing all neognaths except the Galloanserae, has been named Neoaves by Sibley et al. (1988) or Plethornithae by Groth and Barrowclough (1999). The name Neoaves has also been used as the name for the clade containing all neognathous birds (Sibley and Ahlquist 1990; Sibley and Monroe 1990).

Although the monophyly of Neoaves seems well supported, the interrelationships within the group are less well understood. Herein, we study the phylogenetic relationships within a group of neognath taxa referred to by Olson (1985) as the ‘higher land bird assemblage’. This group corresponds to the Anomalogonatae of Beddard (1898) which includes the orders Strigiformes, Caprimulgiformes, Apodiformes, Coliiformes, Trogoniformes, Coraciiformes, Piciformes and Passeriformes (taxonomy follows Wetmore (1960)). The Anomalogonatae thus consists of more than two-thirds of all living bird species. Although rarely demonstrated within a phylogenetic systematic framework, it is commonly assumed that most families included in the Anomalogonatae are monophyletic while several of the orders possibly are not (Burton 1984; Olson 1985). Moreover, the monophyly for the entire group Anomalogonatae is inferred solely from the shared lack of the ambiens muscle. However, this muscle has been lost in certain other birds, e.g. pelicans, herons, some pigeons and doves, and most parrots (George and Berger 1966). Furthermore, monophyly of the Anomalogonatae was not corroborated by DNA-DNA hybridization data (Sibley and Ahlquist 1990). The questionable monophyly of the Anomalogonatae, and the fact that the group has been poorly sampled in previous phylogenetic studies based on DNA sequence data, makes the

taxonomic delimitation of the ingroup difficult (see Material and methods).

Several phylogenetic hypotheses have been presented for the ‘higher land bird assemblage’ (e.g. Olson 1985), but consensus about their inter-relationships has not yet been reached. Some of the traditionally recognized orders, e.g. Passeriformes and Trogoniformes, are well supported monophyletic clades, whereas the monophyly of others, e.g. the Coraciiformes and Piciformes, are much less certain (Burton 1984; Olson 1985; Sibley and Ahlquist 1990).

Because of stochastic factors, an estimate based on a single gene tree may not accurately reflect the species tree (Pamilo and Nei 1988; Avise 1989). Congruence between different gene trees, supposedly belonging to different linkage groups, increases the probability that the trees actually represent the true phylogeny. Furthermore, although often used in avian phylogenetic studies, mitochondrial genes evolve too fast to provide resolution for more ancient groups of birds (Graybeal 1994; Avise et al. 1994a, b).

The use of slower evolving, nuclear genes may possible overcome these problems. The present study investigates the phylogenetic relationships within the Anomalogonatae based on nucleotide sequence data obtained from two single-copy, nuclear genes, *c-myc* and RAG-1. These relationships have previously not been investigated using nuclear genes. Both genes used in this study have only recently received attention in avian phylogenetics, but have shown promising results in resolving basal divergences in birds (Groth and Barrowclough 1999; Ericson et al. 2000; Irestedt et al. in press).

Material and methods

Taxa examined and choice of outgroup

The taxonomic delimitation of the ingroup is problematic because of the uncertainty regarding the monophyly of the Anomalogonatae and the overall limited understanding of major relationships among neognathous birds. Apart from the loss of the ambiens muscle, very

little has been provided to support the monophyly of the group, although the taxa included in the Anomalognatae by Beddard (1898) are often regarded as closely related. Despite uncertainties regarding their overall relationships, all ingroup taxa are monophyletic relative to the orders Galliformes and Anseriformes of which representatives are used as outgroups.

This study includes 46 terminal taxa, with five species representing the passerine lineage and 35 species representing 24 out of 28 families of nonpasserine families included in the 'higher land bird assemblage'. In addition, three representatives of the Cuculiformes (Cuculidae and Musophagidae) have been included. The trees were rooted using the outgroup rooting method (of Farris 1972; cf. Nixon and Carpenter 1993) with three species representing the orders Galliformes and Anseriformes. Sample information and GenBank accession numbers are given in Table 1. In three taxa, the *c-myc* and RAG-1 sequences have been obtained from different individuals. The sequences of *Anas* and *Coracias* are thus composites of *c-myc* data obtained by us, and previously published RAG-1 sequences (Groth and Barrowclough 1999). The *Gallus* sequence is a composite of the *c-myc* sequence published by Watson et al. (1983), and the RAG-1 sequence published by Groth and Barrowclough (1999).

DNA extraction, PCR and sequencing

Genomic DNA was extracted from tissue or blood using standard techniques of proteinase K/SDS digestion followed by phenol chloroform precipitation, or by QIAamp® DNA extraction kits (Qiagen, Hilden, Germany) following the manufacturer's recommendations.

An approximately 500 bp long fragment of exon 3 of the *c-myc* gene was amplified with the primers *mycEX3D* and *RmycEX3D* (for information on primers see Fig. 1, Table 2). The amplifications were carried out with Ready-To-Go® PCR Beads (Amersham Pharmacia Biotech, Uppsala, Sweden) as 25 µl reactions following the manufacturer's recommendations with a final concentration of each primer of 0.4 µM. The following thermocycling conditions were used for the amplification: the samples were initially heated to 94°C for 5 min, followed by 40 cycles of 94°C for 40 s, 49°C for 40 s, and 72°C for 60 s, and ended with a final extension period of 5 min at 72°C. From this first amplification, 1 µl was used as template for a second amplification using primers *mycEX3A* and *RmycEX3A*. The same thermal conditions as in the first round of amplification were used, except that the number of cycles was reduced to 30.

The amplification of the protein-coding RAG-1 gene was performed with combinations of primers R17, R22, R50 and R51, which yielded a fragment of approximately 1000 bp (Fig. 1, Table 2). The reactions were carried out with Ready-To-Go® PCR Beads (Amersham Pharmacia Biotech) as described above, with the following thermocycling conditions: the samples were preheated to 94° for 5 min, followed by four cycles of 94°C for 40 s, 63°C for 1 min, 72°C for 1 min. After this followed another four cycles identical to the preceding cycles, with the exception of a reduction of the annealing temperature to 60°C. In a final round of 32 cycles the annealing temperature was further reduced to 55°C. The procedure was completed by a final extension of 5 min at 72°C.

Before sequencing, the polymerase chain reaction (PCR) products were cleaned with QIAquick PCR Purification Kit (Qiagen). Sequencing of both genes was performed using Perkin Elmer Applied BioSystems (CA, USA) 373 or 377 automated fluorescent sequencing instrument, and Perkin Elmer Applied BioSystems PRISM terminator cycle sequencing kits with AmpliTaq FS polymerase with either dRhodamine or BigDye terminators. The amplified *c-myc* fragment was sequenced in both directions with the primers *mycEX3A*, *RmycEX3A*, *mycEX3C-1* and *RmycEX3B*, and the RAG-1 gene with the primers R17, R22, R50, R51, R52 and R53. Sequence assembly was performed using the Perkin Elmer Applied BioSystems Sequence Navigator program, or SeqMan® 4.00 DNASTAR Inc (WI, USA). All positions have been read in both directions except in a few species where only one strand was possible to read near the end of the sequences. In the *c-myc* gene the nucleotide base could not be determined with certainty in nine cases (0.04%). The corresponding figure for RAG-1 is 47 (0.11%). Some of these ambiguities might reflect actual heterozygosity of the genes, whereas others may be attributed to PCR or sequencing artifacts. All ambiguous positions were treated as uncertainties in the phylogenetic analyses.

Alignment and sequence properties

The sequences were aligned by eye. Due to sequence length differences, gaps were required at two positions to obtain a correct alignment of the *c-myc* sequences. First, one insertion of 12 basepairs (four amino acids) was needed in *Apus apus* (Apodidae), *Hemiprocne longipennis* (Hemiprocidae), and in *Helimaster furcifer*, *Hylocharis chrysurus* and *Phaethornis pretrei* (Trochilidae). The placement of this insertion is not obvious, and it can be inserted at three different positions (at positions 772, 784, or 796, relative to the published chicken sequence (Watson et al. 1983)). However, irrespective of the placement of this insertion the same topology is obtained in the phylogenetic analyses. In addition, a 6 bp deletion was needed at position 889 in *Dendrocopos major* and *Picumnus cirratus* (Picidae).

The analysed part of *c-myc* exon 3 is 489 bp long, corresponding to the region between position 759 and 1235 of the published chicken *c-myc* sequence (Watson et al. 1983). Of the 489 nucleotides, 328 (67%) were found to be invariant between taxa, 52 (11%) variable but uninformative, and 109 (22%) phylogenetically informative.

The sequence obtained from the RAG-1 gene corresponds to the 930 bp between position 1054 and 1983 of the chicken sequence (Carlson et al. 1991). Of these, 499 (54%) positions were invariant, 88 (9%) uninformative, and 343 (37%) phylogenetically informative. The combined, aligned data set consists of 1419 basepairs corresponding to 473 amino acids. In no cases were nonsense or stop codons observed.

The pairwise sequence divergence between taxa was expressed as the uncorrected ('p') distances. To test the level of saturation due to multiple substitutions, the observed pairwise number of transitions (ti) and transversion (tv), respectively, were plotted against the uncorrected sequence distances.

Phylogenetic analysis

The phylogenetic analyses of the aligned sequences were performed with PAUP* 4.0b3 (Swofford 1998) under the parsimony criterion. The genes were analysed both separately and combined. The search for minimum length tree(s) was conducted with heuristic search using 500 random taxon additions and TBR branch swapping. The gaps in the *c-myc* and the combined data sets were coded as missing data, but one extra character was added to the *c-myc* sequence to code for the extra event of the insertion in Apodidae, Hemiprocidae, and Trochilidae, and one for the deletion in the Picidae. Support for individual clades was estimated by parsimony jackknifing (Farris et al. 1996) with Xac: Parsimony Jackknifer (Farris 1997) with 1000 replicates, 10 random additions, and branch swapping. Clades receiving less support than 50% are regarded as unsupported. In addition, Bremer support values (Bremer 1998, 1994) were calculated using TreeRoot, v2 (Sorenson 1999).

Results

Pairwise sequence divergences and saturation analysis

In the *c-myc* gene the smallest sequence divergence, 0.6%, was observed between the motmots, *Momotus* and *Baryphthengus* (Table 3). The largest, 12.3%, was observed between *Gallus* and *Picumnus*. Among the ingroup taxa, the largest divergence, 8.9%, was observed between *Picumnus* and *Tockus*. Also in the RAG-1 gene the least divergence, 1.0%, was found between the two motmot species (Table 4). The largest divergence observed, 15.3%, was found between *Hylocharis* and *Trachyphonus*. This distance is almost identical to that between *Hylocharis* and *Gallus*, 15.2%.

The number of transitions and transversions observed between pairs of taxa are shown in Tables 3 and 4. The transition : transversion ratios calculated from these figures vary between 0 and 30 in *c-myc*, and between 1.4 and 8.5 in RAG-1. The large variation in the *c-myc* ratios is caused by the low number (often zero) of pairwise transversions observed.

In the saturation plots for both genes (Fig. 2a,b) transitions and transversions are roughly linearly correlated against the

Table 1. Samples used in the study

Species	Family	Order	Sample no.	Owner	GenBank Accession No. (c-myc)	GenBank Accession No. (RAG-1)	References
<i>Corythaixoides leucogaster</i>	Musophagidae	Cuculiformes	P509	ZMCU	AF295126	AF294654	
<i>Cuculus camorus</i>	Cuculidae	Cuculiformes	996341	NRM	AF295127	AF294655	
<i>Playa cayana</i>	Cuculidae	Cuculiformes	937230	NRM	AF295128	AF294656	
<i>Asio flammeus</i>	Strigidae	Strigiformes		S. Dunham	AF295129	AF294657	
<i>Glauucidium brasilianum</i>	Strigidae	Strigiformes	937343	NRM	AF295130	AF294658	
<i>Nyctibius aethereus</i>	Nyctibiidae	Caprimulgiformes	B11236	LSUMZ	AF295131	AF294659	
<i>Podager nacunda</i>	Caprimulgidae	Caprimulgiformes	947016	NRM	AF295132	AF294660	
<i>Eurostodopus macrotis</i>	Caprimulgidae	Caprimulgiformes	P393	ZMCU	AF295133	AF294661	
<i>Podargus strigoides</i>	Podargidae	Caprimulgiformes		S. Dunham	AF295134	AF294662	
<i>Steatornis carpinensis</i>	Steatornithidae	Caprimulgiformes	B7474	LSUMZ	AF295135	AF294663	
<i>Apus apus</i>	Apodidae	Apodiformes	P3	ZMCU	AF295136	AF294664	
<i>Hemiprocne longipennis</i>	Hemiprocnidae	Apodiformes	1273	ANSP	AF295137	AF294665	
<i>Helioaster furcifer</i>	Trochilidae	Apodiformes	966911	NRM	AF295138	AF294666	
<i>Hylocharis chrysura</i>	Trochilidae	Apodiformes	937161	NRM	AF295139	AF294667	
<i>Phaethornis pretrei</i>	Trochilidae	Apodiformes	967134	NRM	AF295140	AF294668	
<i>Colius striatus</i>	Coliidae	Coliiformes	P398	ZMCU	AF295141	AF294669	
<i>Trogon melanurus</i>	Trogonidae	Trogoniformes	P494	ZMCU	AF295142	AF294670	Irestedt et al. (in press)
<i>Harpactes diardii</i>	Trogonidae	Trogoniformes	968171	NRM	AF295167	AF295167	
<i>Alcedo atthis</i>	Alcedinidae	Coraciiformes	937351	NRM	AF294671	AF294671	
<i>Chloroceryle americana</i>	Alcedinidae	Coraciiformes	B11311	NRM	AF295144	AF294672	
<i>Todus mexicanus</i>	Todidae	Coraciiformes		LSUMZ	AF295145	AF294673	
<i>Momotia momota</i>	Momotidae	Coraciiformes		NRM	AF295170	AF295170	Irestedt et al. (in press)
<i>Baryphthengus ruficapillus</i>	Momotidae	Coraciiformes	937325	NRM	AF295146	AF294674	
<i>Merops viridis</i>	Meropidae	Coraciiformes	P935	ZMCU	AF295147	AF294675	
<i>Coracias caudata</i> (c-myc)	Coraciidae	Coraciiformes	750	NMWM	AF295148		
<i>Coracias caudata</i> (RAG-1)	Coraciidae	Coraciiformes		FMNH	AF143737		Groth and Barrowclough (1999)
<i>Brachypteracias leptosomus</i>	Brachypteraciidae	Coraciiformes	345686	ZMCU	AF294676	AF294676	
<i>Rhinopomastus cyanomelas</i>	Phoeniculidae	Coraciiformes	P916	ZMCU	AF295150	AF294677	
<i>Upupa epops</i>	Upupidae	Coraciiformes	P502	ZMCU	AF295151	AF294678	
<i>Toxolites erythrorhynchus</i>	Bucerotidae	Coraciiformes	P487	ZMCU	AF295152	AF294679	
<i>Nystaltes maculatus</i>	Bucconidae	Piciformes	947240	NRM	AF295153	AF294680	
<i>Bucco capensis</i>	Bucconidae	Piciformes		T.J. Parsons	AF295154	AF294681	
<i>Galbula cyanescens</i>	Galbulidae	Piciformes		T.J. Parsons	AF295155	AF294682	
<i>Trachyphonus usambiro</i>	Capitomidae	Piciformes	P603	ZMCU	AF295156	AF294683	
<i>Stactolaema olivacea</i>	Capitomidae	Piciformes	P593	ZMCU	AF295157	AF294684	
<i>Eubucco bourcierii</i>	Capitomidae	Piciformes	P587	ZMCU	AF295158	AF294685	
<i>Pteroglossus castanotis</i>	Ramphastidae	Piciformes	937285	NRM	AF295159	AF294686	
<i>Picumnus cirratus</i>	Picidae	Piciformes		AF295174	AF295174		Irestedt et al. (in press)
<i>Dendrocopos major</i>	Picidae	Piciformes		AF295186	AF295186		Irestedt et al. (in press)
<i>Pitta angolensis</i>	Pittidae	Passeriformes		AF295176	AF295176		Irestedt et al. (in press)
<i>Rhinocrypta lanceolata</i>	Rhinocryptidae	Passeriformes		AF295178	AF295178		Irestedt et al. (in press)
<i>Tyrannus savana</i>	Tyrannidae	Passeriformes		AF295182	AF295203		Irestedt et al. (in press)
<i>Menura novaehollandiae</i>	Menuridae	Passeriformes		AF295169	AF295169		Irestedt et al. (in press)
<i>Campephaga flava</i>	Campephagidae	Passeriformes		AF295162	AF295162		Irestedt et al. (in press)
<i>Alectura lathami</i>	Megapodidae	Galliformes		AF295162	AF295162		Irestedt et al. (in press)
<i>Gallus gallus</i> (c-myc)	Phasianidae	Galliformes		LSUMZ	AF296417		Watson et al. (1983)
<i>Gallus gallus</i> (RAG-1)	Phasianidae	Galliformes	B20851	J00889		AF143730	Groth and Barrowclough (1999)
<i>Anas platyrhynchos</i> (c-myc)	Anatidae	Anseriformes		T.J. Parsons		AF143729	Groth and Barrowclough (1999)
<i>Anas strepera</i> (RAG-1)	Anatidae	Anseriformes		T.J. Parsons		AF295160	Groth and Barrowclough (1999)

ANSP, Academy of Natural Sciences of Philadelphia; FMNH, Field Museum of Natural History, Chicago; NRM, Swedish Museum of Natural History, Department of Vertebrate Zoology; ZMCU, University of Copenhagen, Zoological Institute, Department of Population Biology; LSUMZ, Louisiana State University, Museum of Natural Science; NMWM, National Museum of Namibia.

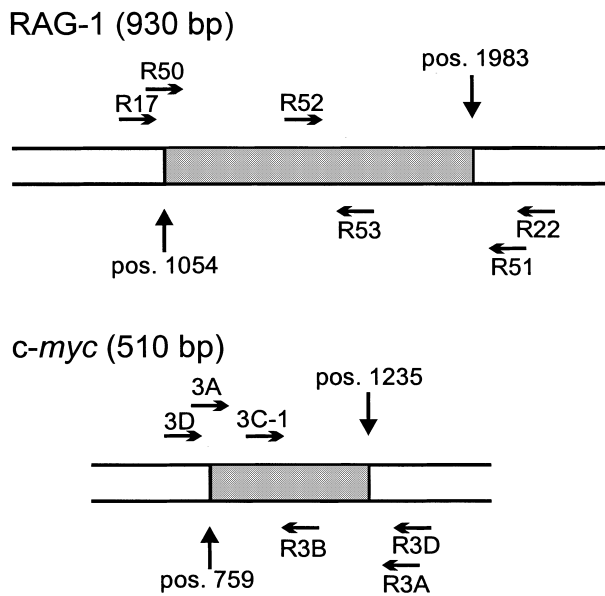


Fig. 1. Positions of the PCR and sequencing primers relative the amplified fragment of each gene. Nucleotide numbers refer to the homologous position in the published chicken sequence (Watson et al. 1983, Carlson et al. 1991)

uncorrected pairwise sequence distances, with no obvious tendency to level off. Similar patterns have been found among passerine birds for both genes (Irestedt et al. 2000), and in RAG-1 between even more distantly related groups, such as birds and crocodylians (Groth and Barrowclough 1999). A faster rate of mutations in RAG-1 is indicated when plotting the pairwise sequence divergence observed for the two genes against each other (Fig. 3). Most data points fall well above the dashed line that indicates a 1 : 1 ratio between the mutational rates of the two genes.

Phylogenetic analysis

The analysis of *c-myc* yielded five trees with a length of 508 steps (Consistency Index (CI) 0.31, Retention Index (RI) 0.54). In the strict consensus of these five trees (Fig. 4) monophyly is not supported for any of the traditionally recognized orders, except the Passeriformes. The passeriform clade is recovered in less than 50% of the jackknife replicates, however. A 100% jackknife support was obtained for a clade consisting of the representatives of the families Picidae (*Picumnus* and *Den-*

drocopos), Capitonidae (*Trachyphonus*, *Stactolaema*, *Eubucco*), and Ramphastidae (*Pteroglossus*) (Fig. 4). Within this clade, the Picidae is the sister-group of the Ramphastidae and Capitonidae, although the Capitonidae was not recovered as monophyletic. The South American capitonid, *Eubucco*, is the sister-group to Ramphastidae, and these in turn form the sister-group to the two African capitonids *Trachyphonus* and *Stactolaema*. Other clades receiving jackknife support are the Cuculidae (*Cuculus* and *Piaya*, 91%), Strigidae (*Glaucidium* and *Asio*, 91%), Trogonidae (*Harpactes* and *Trogon*, 63%), Momotidae (*Baryphthengus* and *Momotus*, 100%), and Bucconidae (*Bucco* and *Nystalus*, 86%). The Trochilidae (*Phaethornis*, *Helimaster* and *Hylocharis*) has a 97% jackknife support. Within the Trochilidae *Phaethornis* is the sister to *Helimaster* and *Hylocharis*. High support values are also found for sister-group relationships between Apodidae (*Apus*) and Hemiprocnidae (*Hemiprocne*) (94%), and Phoeniculidae (*Rhinopomastus*) and Upupidae (*Upupa*) (99%), respectively.

A clade recognized in the strict consensus tree, but not receiving jackknife support consists of the Bucerotidae (*Tockus*), the swifts and treeswifts (Apodidae and Hemiprocnidae), and all caprimulgiforms (except the Nyctibiidae, *Nyctibius*). The *c-myc* data also indicates the existence of a larger clade consisting of the Passeriformes (*Pitta*, *Rhinocrypta*, *Tyrannus*, *Menura* and *Campephaga*), Bucconidae (*Bucco* and *Nystalus*), Galbulidae (*Galbula*), Coraciidae (*Coracias*), Brachypteraciidae (*Brachypteracias*), Coliidae (*Colius*), Cuculidae, Trochilidae and Nyctibiidae. No jackknife support was obtained for this clade, however.

In the analysis of the RAG-1 gene, 87 trees with a length of 1520 steps (CI 0.36, RI 0.52) was obtained. In the strict consensus tree calculated from these trees (Fig. 5), all clades that are well supported in the *c-myc* gene tree are found. Some clades with no support in the *c-myc* gene tree, as the Caprimulgidae (*Podager* and *Eurostopodus*) and the Passeriformes, are supported in the RAG-1 gene tree with values of 89 and 69%, respectively. Other clades in the *c-myc* gene tree with low jackknife support are not found in the RAG-1 gene tree. Although the RAG-1 strict consensus tree is far less resolved than that for *c-myc*, more clades with jackknife support are found in the RAG-1 gene tree. The monophyly of the Alcedinidae (*Alcedo* and *Chloroceryle*) is supported with a 98% jackknife support. Other taxonomic arrangements receiving jackknife supports are the Momotidae and Todidae (*Todus*) (86%), Coraciidae and Brachypteraciidae (94%), and the Phoeniculidae and Upupidae plus the Bucerotidae (75%).

Primer	Sequence (5' to 3')	Reference	Table 2. PCR and sequencing primers
<i>c-myc</i>			
<i>myc</i> EX3D	GAAGAAGAACAAGAAGAAGATG	Ericson et al. (2000)	
<i>Rmyc</i> EX3D	ACGAGAGTTCCTTAGCTGCT	Ericson et al. (2000)	
<i>myc</i> EX3A	CAAGAAGAAGATGAGGAAAT	Ericson et al. (2000)	
<i>Rmyc</i> EX3A	TTAGCTGCTCAAGTTTGTG	Ericson et al. (2000)	
<i>myc</i> EX3C-1	CAAAAAGGCTAAAGTTGG	This study	
<i>Rmyc</i> EX3B	CGGTTGTTGCTGATCTG	Irestedt et al. (in press)	
RAG-1			
R17	CCCTCCTGCTGGTATCCTTGCTT	Groth and Barrowclough (1999)	
R22	GAATGTTCTCAGGATGCCTCCCAT	Groth and Barrowclough (1999)	
R50	CTGATCTGGTAACCCCAAGTAAAATCC	Irestedt et al. (in press)	
R51	GACCCTCTTTCTGCTATGAGGGGGC	Irestedt et al. (in press)	
R52	CAAGCAGATGAAYTGGAGGC	Irestedt et al. (in press)	
R53	TCCATGTCCTTTAAGGCACA	Irestedt et al. (in press)	

Table 3. c-myc. Pairwise sequence divergence (uncorrected distances, below diagonal), and observed numbers of transitions and transversions (ti – tv, above diagonal)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	18-1	19-3	20-4	22-7	21-4	18-4	18-2	20-1	17-3	19-2	19-3	24-1	26-1	27-1	19-2	23-3	17-3	23-3	28-0
2	4.0	7-2	17-3	20-6	21-3	21-3	18-1	24-2	22-2	23-3	23-4	24-2	24-2	23-2	18-1	19-2	23-2	17-4	22-1
3	4.6	1.9	16-5	19-8	16-5	21-5	19-3	22-4	23-4	22-5	23-4	19-4	19-4	18-4	19-3	18-3	18-4	16-6	21-3
4	5.0	4.2	4.4	9-3	15-6	16-6	16-4	18-5	22-5	13-6	17-7	19-5	19-5	20-5	17-4	17-5	17-5	10-6	17-4
5	6.1	5.5	5.7	2.5	18-9	16-7	18-7	22-7	25-8	23-9	21-10	22-8	22-8	23-8	18-7	21-8	21-8	17-10	22-7
6	5.2	5.0	4.4	4.4	5.7	17-6	21-4	18-5	25-5	19-6	19-7	17-5	17-5	18-5	19-4	22-5	17-5	17-7	23-4
7	4.6	5.0	5.5	4.6	4.8	2.9	12-2	18-5	17-5	17-6	17-7	20-5	22-5	21-5	20-4	15-5	18-7	18-7	20-4
8	4.2	4.0	4.6	4.2	5.2	5.2	4.8	16-3	14-3	15-4	17-5	21-3	24-3	21-3	22-2	15-3	17-3	19-5	24-2
9	4.4	5.5	5.5	4.8	6.3	4.8	4.0	4.6	16-4	14-3	14-4	22-2	20-2	19-2	21-3	20-2	16-2	22-4	30-1
10	4.2	5.0	5.7	5.7	6.9	4.6	3.6	4.2	4.2	15-5	17-6	24-4	28-4	23-4	22-3	19-4	15-4	21-6	25-3
11	4.4	5.5	5.7	4.0	6.7	5.2	4.8	3.6	4.2	4.4	8-1	18-3	20-3	22-3	17-4	16-5	15-4	17-5	21-2
12	4.6	5.7	5.7	5.0	6.5	5.4	4.6	3.8	4.8	1.8	4.9	20-4	22-4	22-4	19-5	20-6	16-5	19-6	25-3
13	5.2	5.5	4.8	5.1	6.3	4.6	5.3	5.0	5.9	4.3	4.7	1.2	6-0	9-0	21-3	23-4	18-4	21-4	22-1
14	5.7	5.5	4.8	5.0	6.3	4.6	5.7	4.6	6.7	4.7	5.3	1.8	2.2	11-0	21-3	23-4	22-4	22-4	24-1
15	5.8	5.2	4.6	5.2	6.5	4.8	5.4	4.4	5.6	5.1	5.3	5.0	5.0	6.1	26-3	24-4	21-4	22-4	25-1
16	4.4	4.0	4.6	4.4	5.3	4.8	5.0	5.0	5.2	4.4	5.0	5.0	5.0	5.9	4.6	19-3	20-3	18-5	22-2
17	5.5	4.8	4.6	4.6	6.1	4.2	3.8	4.6	4.6	4.4	5.4	5.7	5.7	5.9	4.6	4.6	12-0	18-6	21-3
18	4.2	5.2	4.6	4.6	4.8	4.2	4.2	4.0	4.0	4.2	4.6	4.8	5.6	5.4	4.8	2.5	4.8	17-6	23-3
19	5.5	4.4	4.6	3.4	5.7	5.0	5.3	5.5	5.7	4.6	5.2	5.3	5.5	5.4	4.9	5.0	4.8	4.2	17-3
20	5.9	4.8	5.0	4.4	6.1	5.7	5.0	6.5	5.9	4.8	5.9	4.8	5.2	5.4	5.0	5.0	5.5	4.2	2.9
21	3.8	4.8	4.6	4.6	6.5	4.6	4.6	4.8	4.4	3.6	4.2	3.6	4.4	4.6	4.8	4.6	3.4	4.8	4.8
22	4.6	5.7	6.3	4.2	5.9	6.1	4.2	4.4	6.1	5.2	5.9	6.1	5.7	6.3	5.7	5.9	5.5	4.8	5.9
23	4.8	5.0	5.7	3.8	5.9	4.4	5.2	4.6	6.3	5.0	5.7	5.9	5.5	6.1	5.5	5.7	5.7	4.2	5.2
24	4.8	5.9	5.7	5.7	7.1	4.8	5.2	5.5	4.8	4.6	5.7	5.1	5.9	5.2	5.5	4.8	4.4	5.0	4.8
25	4.8	4.4	4.6	5.0	6.5	4.4	5.0	4.6	5.5	5.5	5.7	5.7	5.9	5.2	5.3	5.5	4.8	4.8	5.9
26	4.8	4.6	4.4	3.8	5.5	4.6	4.0	4.8	4.6	4.2	5.2	4.4	4.8	4.6	4.0	4.4	4.4	4.2	4.4
27	7.3	6.5	6.7	6.3	8.6	7.3	8.0	7.1	6.5	6.1	7.5	6.1	6.1	6.3	7.6	6.3	7.1	6.3	6.3
28	7.2	7.6	7.3	6.9	8.0	7.4	6.9	5.5	6.7	5.9	7.8	6.7	6.7	6.5	7.2	5.7	6.9	6.7	7.1
29	5.0	6.1	6.5	6.3	7.3	5.0	4.6	5.7	5.0	5.3	5.5	6.9	7.3	7.1	5.9	5.9	5.2	7.1	7.1
30	5.7	5.2	4.4	5.7	6.1	5.5	5.0	5.5	5.9	4.6	5.2	4.4	5.0	4.4	4.6	4.4	5.0	5.0	5.2
31	5.0	5.0	4.4	5.0	5.9	4.8	5.2	5.1	5.2	5.7	5.9	4.2	4.4	4.6	4.2	4.8	4.0	4.4	5.0
32	5.5	5.0	4.6	5.0	6.5	6.7	6.7	5.2	5.9	5.0	5.9	5.3	5.2	5.4	4.6	5.2	5.0	5.7	5.9
33	5.7	4.6	4.4	3.8	5.0	5.2	5.0	5.9	5.5	4.0	5.2	4.2	4.6	5.2	4.4	4.8	4.6	4.0	4.2
34	7.5	6.3	6.1	5.3	6.5	6.9	6.3	6.5	6.7	5.5	7.1	6.5	6.1	6.7	5.7	5.7	6.3	6.1	6.3
35	5.9	5.5	4.8	4.4	6.3	4.8	5.0	4.6	5.2	3.8	5.0	4.4	5.3	5.5	4.8	4.4	4.2	4.4	5.2
36	5.5	5.0	4.6	4.4	6.3	4.8	5.5	6.1	5.7	4.2	5.2	5.3	5.7	6.3	4.8	4.8	4.6	4.4	5.7
37	7.5	5.7	5.5	5.3	7.2	6.4	6.4	7.0	7.0	6.2	6.8	6.6	7.0	6.4	6.6	5.8	6.4	5.8	6.6
38	6.4	6.0	5.3	4.7	5.8	5.7	4.5	5.3	5.9	5.1	5.3	6.0	6.0	6.2	5.4	4.7	5.3	5.3	6.4
39	6.3	5.3	4.8	4.6	6.1	5.3	5.0	5.7	6.6	5.5	6.5	5.3	4.8	5.0	4.2	5.3	6.3	5.1	5.0
40	6.3	4.8	4.6	5.1	6.5	5.5	5.7	5.5	6.3	5.0	5.7	5.3	5.3	4.6	4.9	4.8	5.7	5.3	4.8
41	6.7	5.2	4.6	5.7	6.1	5.7	5.9	6.1	6.7	6.9	7.1	5.5	5.0	4.8	5.2	5.9	5.9	5.7	5.8
42	5.7	6.5	6.3	6.7	8.2	6.3	6.5	6.5	6.5	6.7	7.3	5.9	6.1	5.4	6.3	6.9	6.3	6.1	6.9
43	6.3	6.1	5.5	5.9	6.5	5.9	6.1	6.3	7.1	6.9	7.1	6.1	6.3	5.3	6.5	6.5	6.3	6.1	6.7
44	7.5	8.4	8.2	8.8	9.6	9.0	8.2	7.8	8.4	7.6	8.2	8.4	7.9	9.2	8.6	8.4	8.2	8.6	9.2
45	8.6	10.1	10.7	9.5	11.3	9.9	9.0	8.6	8.6	7.6	8.6	9.4	9.2	10.0	9.7	9.9	9.2	8.6	9.2
46	5.7	7.3	7.1	7.8	8.2	8.0	6.7	6.9	6.7	6.9	7.1	7.3	7.3	7.1	6.9	7.1	6.3	6.9	8.2

Table 3. (Continued)

21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
18-0	22-0	23-0	22-1	19-4	21-2	30-5	30-4	18-6	27-0	24-0	22-4	24-3	29-7	24-4	22-4	28-7	25-5	28-2	26-4	29-3	19-8	23-7	29-7	34-7	23-4
22-1	26-1	23-1	26-2	18-3	21-1	25-6	31-5	24-5	24-1	23-1	21-3	20-2	24-6	23-3	21-3	21-6	24-4	23-2	18-5	23-2	24-7	23-6	32-8	40-8	30-5
19-3	27-3	24-3	23-4	17-5	18-3	24-8	28-6	26-5	18-3	18-2	17-5	17-4	21-8	18-5	17-5	18-8	19-6	19-4	15-7	18-4	21-9	18-8	29-10	41-10	27-7
18-4	16-4	14-4	22-5	18-6	14-4	21-9	25-8	24-6	23-4	20-4	18-6	13-5	18-7	15-6	15-6	16-9	15-7	17-5	16-8	22-5	23-9	20-8	31-11	34-11	29-8
24-7	21-7	21-7	26-8	22-9	19-7	29-12	27-11	26-9	22-7	21-7	22-9	16-8	21-10	21-9	21-9	22-12	17-10	21-8	20-11	21-8	26-13	19-12	32-14	40-14	28-11
18-4	25-4	26-4	25-5	15-6	18-4	26-9	30-8	23-8	23-4	20-4	21-6	20-5	24-9	17-6	17-6	21-9	20-7	20-5	18-8	22-5	20-10	19-9	32-11	36-11	30-8
18-4	16-4	17-4	18-5	18-6	15-4	29-9	27-8	18-6	22-4	19-4	26-6	19-5	21-9	18-6	20-6	21-9	16-5	19-5	19-8	23-5	21-10	20-9	28-11	32-11	24-8
20-2	22-2	23-2	22-3	20-4	15-2	27-7	27-6	18-4	22-2	23-2	21-4	19-3	21-7	18-4	20-4	21-7	22-3	24-3	19-6	25-3	23-8	22-7	28-9	32-9	28-6
22-1	20-1	21-1	26-0	17-5	20-3	27-4	23-3	20-7	25-1	23-1	20-5	24-4	23-8	24-5	24-5	25-8	22-6	22-3	21-5	25-4	22-9	24-6	25-8	32-8	28-5
18-3	26-3	27-3	19-4	21-5	19-3	26-8	25-7	17-7	25-3	22-3	23-5	22-4	24-8	20-5	22-5	25-8	25-6	27-4	23-7	28-4	22-9	24-6	30-10	31-10	25-7
15-2	23-2	22-2	19-3	20-6	16-4	22-7	22-6	17-8	20-2	22-3	18-6	14-5	17-9	12-6	14-6	20-9	17-7	21-4	18-6	28-5	22-10	24-9	31-5	31-5	29-4
17-3	25-3	24-3	23-4	20-7	20-5	28-8	30-6	19-7	22-3	25-3	21-7	19-6	24-10	17-7	18-7	22-10	17-8	26-5	20-7	28-6	24-11	24-10	33-6	35-6	29-5
16-1	28-1	27-1	22-2	22-5	18-3	23-6	27-5	26-7	20-1	19-1	20-5	16-4	23-8	16-5	20-5	23-8	22-6	21-3	20-5	22-4	19-9	21-8	32-8	37-8	30-5
20-1	26-1	25-1	26-2	23-5	20-3	23-6	27-5	28-7	23-1	20-1	20-5	18-4	21-8	20-5	22-5	25-8	22-6	19-3	20-5	20-4	20-9	22-8	30-8	36-8	30-5
21-1	29-1	28-1	23-2	20-5	19-3	24-6	26-5	27-7	20-1	21-1	21-5	21-4	24-8	21-5	25-5	22-8	23-6	20-3	17-5	19-4	17-9	17-8	36-8	40-8	29-5
21-2	25-2	24-2	23-3	21-4	17-2	29-7	28-6	22-6	20-2	18-2	18-4	18-3	20-7	19-4	19-4	24-7	20-5	17-3	17-6	22-3	22-8	24-7	32-9	37-9	27-6
19-3	25-3	24-3	21-2	21-5	18-3	24-6	22-5	21-7	18-3	20-3	20-5	19-4	19-8	16-5	18-5	19-8	16-6	21-4	16-7	24-4	24-9	25-6	30-10	37-10	27-7
13-3	23-3	24-3	19-2	18-5	18-3	27-6	27-5	18-7	21-3	16-3	19-5	18-4	22-8	15-5	17-5	22-8	19-6	26-4	20-7	24-4	21-9	24-6	29-9	34-9	23-6
17-3	20-3	17-3	20-4	18-5	15-5	22-8	25-7	25-9	21-3	18-3	20-7	13-6	19-10	14-7	14-7	17-10	17-8	18-5	18-7	21-6	22-7	23-6	31-10	33-8	26-7
14-0	28-0	25-0	22-1	24-4	19-2	25-5	30-4	22-6	23-0	20-0	20-4	17-3	23-7	21-4	23-4	24-7	25-5	22-2	19-4	25-3	25-8	25-7	37-7	37-7	35-4
	26-0	25-0	16-1	17-4	15-2	26-5	30-4	22-6	23-0	20-0	20-4	18-3	25-7	18-4	20-4	23-7	22-5	25-2	21-4	25-3	19-8	25-7	31-7	32-7	29-4
5.5	3-0	3-0	26-1	24-4	19-2	34-5	32-4	30-6	33-0	28-0	25-4	26-3	27-7	28-4	28-4	29-7	24-5	24-2	23-4	29-3	29-8	29-7	36-7	37-7	33-4
5.2	0.6	5.7	25-1	25-4	20-2	31-5	31-4	31-6	32-0	27-0	24-4	24-3	27-7	26-4	26-4	27-7	22-5	23-2	22-4	28-3	30-8	30-7	37-7	38-7	34-4
3.6	5.7	6.1	5.0	19-5	17-3	30-4	24-3	24-7	25-1	24-1	27-5	24-5	23-8	18-5	22-5	23-8	21-9	23-7	21-5	25-4	19-9	23-6	35-8	31-5	
4.4	5.9	6.1	5.0	5.0	17-2	25-7	27-6	20-8	21-4	18-4	19-6	24-5	22-9	21-4	23-6	21-9	23-7	19-4	17-8	21-5	15-8	20-7	27-9	32-8	
3.6	4.4	4.6	4.2	4.0	6.9	28-5	28-4	21-6	23-2	22-2	22-4	20-3	22-7	17-4	21-4	21-7	23-5	19-2	14-6	22-3	21-8	20-7	33-7	35-7	31-6
6.5	8.2	7.5	7.1	6.7	6.9	3.6	14-3	25-11	29-5	30-5	27-7	20-8	25-12	22-9	22-9	25-10	26-10	29-6	30-9	31-8	27-13	30-10	33-10	34-8	36-9
7.1	7.6	7.4	5.7	5.7	5.7	7.5	7.3	27-7	25-4	28-4	26-8	24-7	21-11	26-8	25-8	31-11	28-7	28-7	25-10	31-7	23-12	28-11	21-13	26-13	30-10
5.9	7.5	7.8	6.5	6.9	5.7	7.1	6.1	6.3	4.2	4.4	16-4	17-4	32-9	22-8	25-4	25-7	20-5	21-2	18-4	16-3	22-8	20-7	34-7	41-7	28-4
4.8	6.9	6.7	5.5	5.2	5.2	7.1	7.1	7.1	1.7	8-0	17-4	18-3	19-7	22-4	24-4	24-7	21-5	20-2	19-4	16-3	19-8	21-7	32-7	38-7	23-4
4.2	5.9	5.7	5.2	4.6	5.0	7.3	6.7	6.5	6.3	6.7	6.5	18-3	19-7	22-4	24-4	24-7	21-5	20-2	19-4	16-3	19-8	21-7	32-7	38-7	23-4
5.0	6.1	5.9	6.7	5.2	5.5	7.1	7.1	7.1	4.2	4.4	4.4	21-5	21-9	22-6	24-6	25-9	23-7	21-4	17-8	20-5	21-10	21-9	33-11	38-11	28-8
4.4	6.1	5.7	5.0	6.1	4.8	5.9	6.5	7.1	4.6	4.4	5.5	2.5	8-4	9-1	9-1	13-6	12-4	19-4	20-7	21-4	22-9	21-8	34-10	38-10	30-7
6.7	7.1	7.1	6.5	6.5	6.1	7.8	6.7	8.6	5.7	5.5	6.3	2.5	4.2	15-5	15-5	15-10	14-8	14-8	19-11	21-8	24-13	21-12	38-14	39-14	33-11
4.6	6.7	6.3	4.8	5.7	4.4	6.5	7.1	6.3	5.2	5.5	5.9	2.1	4.2	4-0	4-0	16-7	15-5	23-5	20-8	24-5	24-10	23-9	32-11	34-11	34-8
5.0	6.7	6.3	5.7	6.1	5.2	6.5	6.9	6.9	6.1	5.9	6.3	2.1	4.2	0.8	0.8	15-7	14-5	25-5	24-8	26-5	26-10	25-9	32-11	34-8	
6.4	7.7	7.2	6.6	6.4	6.0	7.5	8.1	8.9	6.8	6.6	7.2	4.0	5.3	4.9	4.7	9-4	9-4	24-8	21-11	23-8	24-13	22-12	39-13	44-14	34-11
5.7	6.2	5.7	5.9	6.4	6.0	7.7	7.0	7.4	5.1	4.8	5.5	3.4	4.7	4.2	4.0	2.8	2.8	20-6	20-9	20-6	25-11	21-10	36-11	43-12	29-9
5.7	5.5	5.3	5.2	4.8	4.4	7.6	6.5	7.4	5.1	4.8	5.5	5.0	4.6	5.9	6.3	6.8	5.5	20-6	12-2	17-0	18-7	18-6	36-8	40-8	31-6
5.3	5.7	5.5	5.5	5.3	4.2	8.2	7.8	7.4	4.6	4.8	5.3	5.7	6.3	5.9	6.7	6.8	6.2	2.9	12-2	12-3	19-10	16-9	38-11	42-11	31-8
5.9	6.7	6.5	6.1	5.5	5.2	8.2	7.8	8.0	4.6	4.0	5.2	5.2	6.1	6.1	6.5	6.6	5.5	3.6	3.2	5.5	19-7	17-6	34-10	45-10	29-7
5.7	7.8	8.0	5.9	4.8	6.1	8.4	8.2	7.3	6.3	5.7	6.5	6.5	7.8	7.1	7.5	7.9	7.7	5.7	5.9	5.5	20-5	29-15	34-13	26-12	
6.7	7.5	7.8	6.1	5.7	5.7	8.4	8.0	8.2	5.7	5.9	6.3	6.1	6.9	6.7	7.1	7.2	6.6	5.1	5.3	4.8	5.2	20-5	38-14	44-12	28-11
8.0	9.0	9.2	9.0	7.5	8.4	9.0	8.6	7.1	8.6	8.2	9.2	9.2	10.9	9.0	9.0	11.1	10.0	9.5	10.3	9.2	9.2	10.9	15-4	28-9	
8.2	9.2	9.4	8.4	8.2	8.8	8.8	8.6	8.2	10.1	9.4	10.3	10.1	11.1	9.4	10.3	12.3	11.7	10.3	11.1	11.5	9.9	11.7	4.0	7.8	31-9
6.9	7.8	8.0	7.5	7.3	7.8	9.4	9.3	8.4	6.7	5.7	7.5	7.8	9.2	8.8	8.8	9.6	8.1	8.0	8.2	7.5	8.0	8.2	7.8	8.4	

Table 4. RAG-1. Pairwise sequence divergence (uncorrected distances, below diagonal), and observed numbers of transitions and transversions (ti – tv, above diagonal)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	41-11	45-14	32-10	41-10	27-9	30-9	30-7	40-8	39-7	46-21	41-13	85-24	87-26	73-23	56-16	57-11	51-13	45-16	50-15
2	5.6	35-5	40-16	42-15	31-16	43-16	42-14	50-15	48-12	43-28	39-20	84-31	82-33	71-28	55-21	70-14	66-14	48-16	48-16
3	6.3	4.3	51-15	51-16	42-19	52-19	47-17	53-18	52-15	53-29	50-21	89-32	89-34	81-29	59-24	72-17	67-17	57-22	58-19
4	4.6	6.1	7.2	26-5	23-13	37-13	34-13	44-14	33-13	45-25	41-17	83-28	84-30	71-27	54-21	59-15	53-18	45-21	47-20
5	5.5	6.1	7.2	3.4	33-13	46-15	44-11	50-14	46-13	50-25	46-17	86-28	85-30	78-27	61-20	62-14	54-17	47-20	52-19
6	3.9	5.1	6.6	4.0	4.9	30-14	31-12	37-9	33-12	41-26	37-18	81-29	84-31	70-28	48-17	54-16	52-18	41-21	41-18
7	4.2	6.3	7.6	5.5	4.7	3.1	17-12	41-13	42-12	51-25	47-17	74-29	75-31	68-27	53-21	58-16	55-18	48-21	51-20
8	4.0	6.0	6.9	5.2	4.6	5.8	40-11	40-11	41-10	42-24	38-16	76-27	78-29	73-26	48-19	61-14	54-16	50-19	45-18
9	5.2	7.0	7.6	6.4	6.9	5.0	5.5	5.5	47-11	56-25	56-17	86-26	89-28	81-27	58-20	66-13	62-17	62-20	58-17
10	5.0	6.5	7.2	5.1	6.4	4.9	5.8	6.3	8.1	51-23	51-16	84-25	87-29	79-24	56-17	64-14	56-16	55-17	57-18
11	7.2	7.6	8.8	7.6	8.1	7.2	7.1	8.7	8.1	8.1	22-12	83-31	85-31	74-28	64-33	78-25	72-28	58-31	52-32
12	5.8	6.3	7.6	6.4	6.8	5.9	7.0	7.9	7.2	3.7	77-25	77-25	79-27	64-22	62-25	71-17	64-20	51-23	50-24
13	11.7	12.4	13.0	12.1	12.3	11.8	11.1	12.1	11.8	12.3	11.0	1.5	10-4	40-11	83-36	87-29	86-33	83-32	87-34
14	12.2	12.4	13.2	12.4	12.4	11.4	11.5	12.6	12.5	12.5	11.4	12.8	13.2	38-11	85-38	89-31	89-35	85-36	91-37
15	10.3	10.7	11.8	10.7	11.3	10.6	10.3	10.7	11.1	11.0	9.3	5.5	5.3	80-35	86-29	85-32	84-33	74-33	77-34
16	7.7	8.2	8.9	8.2	8.7	7.0	8.0	8.2	7.9	10.4	9.4	12.8	13.2	12.4	10.0	71-21	67-23	59-24	68-23
17	7.4	9.2	9.7	8.2	8.3	7.7	8.1	8.2	8.5	11.3	9.7	12.6	13.0	12.6	10.0	18-6	63-21	67-19	72-20
18	6.9	8.6	9.0	7.8	7.6	7.5	7.9	7.5	7.8	10.8	9.0	12.8	13.3	12.6	9.7	2.6	9.0	7.0	71-22
19	6.6	7.2	8.5	7.2	7.2	6.7	7.4	7.4	7.8	7.8	8.0	12.4	13.0	11.5	8.9	9.4	9.0	7.3	40-13
20	7.0	6.9	8.3	7.3	7.6	6.4	7.6	6.8	8.1	9.0	8.0	13.1	13.8	12.0	9.8	10.0	10.0	5.7	8.8
21	7.3	9.5	9.7	8.7	9.1	8.3	7.1	8.1	8.5	11.4	10.6	13.7	14.3	13.1	9.8	9.6	9.4	8.8	8.8
22	7.4	8.2	9.2	8.1	8.1	7.0	7.8	8.3	7.4	10.9	9.7	12.9	13.8	13.2	9.4	8.8	8.8	8.1	7.2
23	7.7	8.6	9.9	8.3	8.4	7.6	7.8	6.8	9.0	7.9	11.0	13.2	13.8	13.3	9.9	9.5	9.5	8.6	7.9
24	8.8	9.9	10.5	9.5	9.9	8.2	10.0	9.4	9.7	8.8	11.8	13.7	14.1	13.0	10.9	10.8	10.4	11.0	10.4
25	5.5	6.5	8.0	5.7	6.6	5.7	6.8	6.2	6.8	8.9	7.5	13.0	13.7	11.2	8.7	9.1	8.4	7.0	7.3
26	5.3	6.1	7.1	5.9	5.9	4.9	6.0	5.7	6.6	8.5	7.1	12.0	12.4	11.4	8.2	8.1	7.6	7.3	7.1
27	11.2	12.8	13.5	11.4	12.5	11.2	10.8	11.1	11.4	14.7	13.5	13.4	14.1	13.7	11.5	12.5	12.2	12.9	13.0
28	10.2	10.5	11.6	10.0	11.3	9.4	9.6	9.4	10.4	12.9	12.1	13.0	13.1	13.3	10.6	11.8	11.1	11.2	10.5
29	8.6	9.9	11.0	8.6	9.4	8.6	8.0	8.4	8.7	12.6	11.3	14.2	14.5	13.9	10.0	10.7	10.8	10.7	10.5
30	8.5	8.6	9.2	8.9	9.4	7.6	9.0	8.7	9.3	10.3	9.1	12.7	13.1	12.3	9.8	11.0	10.8	9.4	8.5
31	8.6	8.9	8.9	9.3	9.8	7.5	9.0	8.7	9.2	10.5	9.5	13.2	13.6	12.8	9.6	11.1	10.9	9.7	8.8
32	9.1	10.6	11.6	9.9	10.3	9.4	9.7	8.8	8.9	11.5	10.7	13.5	14.4	13.1	11.0	12.2	11.7	10.9	10.9
33	10.8	10.8	11.5	11.2	11.9	10.5	11.1	10.6	10.8	13.6	13.0	14.8	15.3	15.2	11.6	11.9	11.2	12.2	11.5
34	9.8	10.1	10.6	10.1	11.0	9.7	10.2	9.5	9.4	12.4	11.8	13.8	14.3	14.1	11.1	11.0	10.7	10.9	9.9
35	10.4	10.3	10.8	11.0	12.0	10.1	10.5	10.0	10.4	10.8	13.4	13.9	14.4	14.5	11.3	11.8	11.5	11.3	11.5
36	9.7	9.7	10.7	10.2	11.3	9.2	9.9	9.8	9.8	12.9	11.7	13.5	14.0	13.8	10.9	11.3	10.9	10.9	10.6
37	8.8	8.9	9.8	9.2	9.8	8.5	9.2	8.7	9.0	12.0	10.7	13.7	14.0	13.3	10.1	10.3	10.4	10.5	10.0
38	8.7	9.0	9.6	9.4	10.1	8.6	9.5	8.9	9.3	11.8	10.2	14.2	14.5	13.4	10.3	11.0	11.1	9.9	10.1
39	5.2	5.6	6.6	5.8	5.9	4.8	6.3	6.0	6.2	6.0	6.9	10.7	11.3	11.0	8.2	7.4	7.1	7.2	6.9
40	5.7	6.5	7.4	6.5	6.9	5.3	6.7	6.1	6.9	8.4	7.2	11.7	11.5	10.6	8.2	9.0	8.5	8.4	7.9
41	5.6	6.7	7.0	6.7	7.0	5.6	7.0	6.5	7.3	8.4	7.2	11.7	11.8	10.6	8.5	9.6	9.0	8.1	7.9
42	6.0	6.9	8.0	6.9	7.4	5.8	7.0	5.9	6.7	7.2	9.1	11.7	12.3	11.3	8.4	9.2	8.5	7.8	7.8
43	6.0	6.6	7.7	6.6	7.4	5.8	6.4	7.0	6.7	8.6	7.3	11.5	12.0	10.7	7.8	9.3	8.6	7.4	7.6
44	7.9	8.3	9.7	8.7	9.0	6.9	7.9	7.5	8.4	10.7	9.7	14.0	14.0	12.7	10.5	11.1	10.4	10.1	9.8
45	8.8	9.6	10.1	9.4	9.8	8.8	9.1	8.5	9.0	11.3	9.9	15.2	15.2	13.2	11.5	12.3	11.0	11.0	10.8
46	6.0	7.5	9.0	6.7	7.2	6.2	7.0	6.5	6.4	9.1	7.8	13.4	13.3	11.4	9.9	9.9	9.8	8.6	8.4

Table 4. (continued)

54-14	55-14	57-14	64-18	39-12	38-11	81-22	77-18	66-14	54-25	54-26	66-18	82-18	76-15	76-21	72-17	66-14	63-18	39-9	44-9	43-9	45-11	46-10	52-21	60-22	46-10	
69-19	57-19	59-21	67-25	47-13	41-16	92-27	74-23	71-21	52-28	54-29	77-20	79-21	76-18	72-24	69-20	63-17	63-21	38-14	46-14	50-12	48-16	46-15	51-26	62-27	53-17	
68-22	63-22	68-24	69-28	60-14	49-17	94-30	82-25	78-24	57-29	53-30	84-23	85-22	80-19	75-25	77-21	70-18	67-22	44-17	52-17	50-15	55-19	53-18	61-29	64-30	64-20	
61-19	55-19	56-20	63-24	37-15	40-14	77-27	69-23	59-20	54-28	56-29	69-22	80-23	73-20	75-26	71-22	63-19	63-23	38-13	44-15	47-14	47-16	45-15	55-25	58-28	47-14	
69-16	59-16	60-18	60-18	68-24	47-14	42-13	91-24	69-18	62-25	63-28	64-23	89-22	83-19	87-25	83-21	71-18	72-22	41-13	49-15	52-13	56-13	55-14	59-25	63-28	53-14	
58-19	46-18	51-19	55-21	36-17	30-16	76-27	64-23	61-19	43-28	43-28	74-21	75-23	70-20	72-22	66-19	58-19	57-23	30-14	35-14	38-14	38-16	39-15	46-18	57-25	43-15	
47-19	53-19	53-19	70-22	46-17	40-16	72-26	66-22	57-17	54-30	53-31	69-20	80-23	75-20	72-26	69-22	64-19	65-23	46-12	48-14	51-14	49-16	44-15	47-26	58-26	52-13	
51-15	50-15	48-15	66-21	43-15	39-14	77-25	66-21	63-15	55-26	52-29	63-19	77-21	70-18	69-24	70-20	61-17	62-21	43-12	44-12	48-12	43-12	39-11	46-24	56-23	47-13	
59-16	59-18	65-18	68-22	47-16	49-13	84-26	67-22	67-18	57-27	55-28	75-22	76-22	75-19	72-25	69-21	65-16	64-22	44-13	51-13	55-13	47-15	51-14	53-23	58-26	56-14	
62-17	52-17	56-17	60-21	50-12	47-14	79-25	75-21	64-17	58-28	56-29	63-19	79-21	69-18	76-24	74-20	65-17	72-21	43-11	47-12	48-12	43-10	49-13	54-24	59-25	46-13	
75-31	70-31	71-31	76-33	54-29	51-28	100-35	87-33	86-31	58-38	59-39	76-31	93-33	85-30	87-38	85-34	78-37	83-34	75-35	50-24	52-26	54-24	59-26	61-38	68-37	60-25	
76-23	67-23	67-23	80-25	51-19	48-18	97-27	87-25	82-23	55-30	57-31	76-23	94-27	86-24	84-30	82-26	74-23	68-27	46-18	49-18	51-16	53-18	51-17	60-30	63-29	56-17	
95-32	87-33	89-33	89-38	89-32	84-27	87-36	86-34	100-31	79-39	82-40	89-36	99-37	93-34	90-38	87-36	93-32	98-34	70-28	81-27	84-25	79-29	78-28	92-38	104-37	99-25	
99-34	92-36	92-36	91-40	93-34	86-29	92-38	86-36	101-33	81-41	84-42	94-40	102-40	96-37	93-41	90-39	94-34	99-36	73-30	78-29	83-27	83-31	81-30	89-41	101-40	96-28	
89-33	89-33	90-33	85-35	75-29	78-28	93-33	92-31	98-30	76-38	80-39	86-35	104-37	97-34	97-38	91-36	87-33	91-33	73-27	72-26	74-24	77-28	72-27	80-38	88-35	81-25	
69-22	63-24	66-26	73-27	59-22	55-21	76-30	74-24	67-26	64-27	61-28	74-27	86-22	84-19	84-21	83-18	75-17	74-22	57-19	57-19	60-19	57-21	52-20	69-29	77-30	70-22	
71-17	62-19	66-21	74-24	66-17	60-14	87-26	85-22	77-21	71-30	71-31	87-23	86-23	81-20	83-26	81-22	76-17	78-23	53-14	66-16	74-14	68-16	70-15	76-26	88-24	74-17	
66-21	61-20	65-22	69-27	59-19	53-18	85-27	80-23	77-23	72-28	72-29	84-23	81-23	79-20	81-26	78-22	75-19	80-23	49-16	61-18	68-16	61-18	63-17	71-26	79-23	72-19	
62-20	59-16	62-18	74-28	45-20	49-19	86-32	76-28	73-26	54-33	56-34	73-27	87-26	78-23	78-27	73-22	66-26	47-18	58-20	55-18	53-19	52-19	51-18	61-33	70-32	58-22	
63-19	52-15	56-17	71-25	51-17	48-18	89-31	70-27	74-23	49-30	51-31	74-26	86-21	74-18	83-24	77-20	70-21	71-23	46-17	53-20	55-17	52-20	51-19	61-30	67-33	57-21	
52-16	52-18	69-26	59-18	57-15	78-30	77-26	65-22	64-31	62-32	71-25	84-26	80-23	78-29	79-25	80-20	77-26	61-17	67-19	69-17	65-15	57-18	73-31	78-30	73-20		
7.3	1.0	7-2	63-25	54-18	51-15	73-28	74-24	71-22	64-29	61-32	68-25	82-26	79-23	80-29	79-25	72-22	77-26	55-15	63-19	67-17	64-17	60-18	66-29	78-30	63-18	
7.6	9.6	10.2	68-26	56-20	53-17	78-30	77-26	72-22	69-31	66-34	72-24	86-28	83-25	85-31	84-27	76-24	78-28	60-17	65-19	68-19	69-19	63-20	66-29	80-30	67-18	
10.2	9.6	10.2	65-24	65-24	63-23	85-31	79-27	69-26	59-35	62-36	73-26	76-28	76-25	82-31	84-27	80-26	66-23	66-23	65-21	72-23	72-23	66-24	66-33	85-32	76-24	
8.3	7.8	8.2	9.6	9.6	34-9	80-28	74-24	75-22	51-31	53-32	63-25	86-24	82-21	79-27	77-23	76-20	88-24	44-13	54-17	53-17	53-17	46-16	66-32	65-30	54-18	
7.7	7.1	7.6	9.3	4.6	79-23	68-21	68-21	62-21	52-30	50-31	69-24	82-23	80-20	82-26	73-22	68-17	62-23	41-12	47-16	51-14	47-16	42-15	54-28	62-29	49-17	
11.8	10.9	11.7	12.7	11.8	11.1	50-10	50-10	73-30	81-36	79-37	87-29	98-30	94-27	88-33	93-27	91-26	93-30	77-21	90-27	91-25	85-27	76-24	89-37	108-32	93-26	
11.2	10.6	11.1	11.5	10.6	9.6	60-26	60-26	60-26	70-35	68-36	89-26	91-25	89-22	81-28	92-22	84-21	88-25	68-19	75-23	78-21	73-23	66-19	77-32	98-27	87-23	
9.4	10.0	10.2	11.3	9.4	8.9	11.1	9.3	11.2	11.2	9.3	7.7	9.7	32-5	32-11	36-7	56-10	55-12	78-19	83-19	89-21	81-23	81-20	80-35	99-32	94-24	
10.2	10.0	10.8	10.1	8.8	8.8	12.8	12.7	11.2	11.2	11.2	11.3	12.6	11.5	11.1	11.3	11.9	11.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0
10.1	10.0	10.8	10.6	9.2	8.7	12.7	12.7	11.2	11.2	11.2	11.3	12.3	4.6	4.8	34-4	54-7	53-9	70-16	77-18	82-18	73-20	72-17	83-32	94-29	89-21	
10.4	10.1	10.4	10.7	9.6	10.1	12.9	12.9	10.7	9.3	9.7	11.3	12.3	4.6	4.2	24-5	55-13	53-13	76-22	79-24	79-24	79-26	76-23	81-34	95-33	91-27	
11.8	11.6	12.3	11.2	11.9	11.3	13.8	13.8	12.6	11.5	11.1	11.3	12.3	4.6	4.2	24-5	55-13	53-13	76-22	79-24	79-24	79-26	76-23	81-34	95-33	91-27	
11.1	11.0	11.7	10.9	11.1	10.8	13.1	13.1	12.1	11.7	10.5	11.2	4.7	4.2	3.1	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	
11.5	11.7	12.5	12.2	11.4	11.6	13.0	13.0	11.8	11.2	10.5	11.2	4.7	4.2	3.1	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	
11.3	11.3	12.1	12.1	10.9	10.3	13.1	13.1	12.5	11.9	10.2	10.5	11.2	4.7	4.2	3.1	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	
11.1	10.4	11.1	11.8	10.6	9.4	12.9	12.9	11.7	11.4	10.4	10.7	12.3	7.4	6.9	7.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	6.7	
11.1	11.1	11.4	11.4	9.9	9.1	13.4	13.4	12.3	10.9	9.9	10.2	11.7	7.2	6.7	7.1	6.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	
8.5	7.6	8.4	9.7	6.2	5.8	10.8	10.8	9.5	9.4	8.5	8.8	9.9	10.5	9.3	10.6	9.7	9.0	8.8	8.8	8.8	8.8	8.8	8.8	8.8	8.8	
9.3	8.9	9.1	9.3	7.7	6.8	12.8	12.8	10.6	10.5	8.5	8.9	10.0	11.0	10.3	11.1	10.2	9.8	9.5	5.0	25-7	37-14	35-11	50-24	59-25	53-13	
9.3	9.1	9.4	10.3	7.3	7.0	12.6	12.6	10.7	10.6	9.0	9.4	11.0	11.8	10.8	11.1	10.9	10.1	9.9	5.0	25-7	37-14	35-11	50-24	59-25	53-13	
8.6	8.7	9.5	10.3	7.5	6.8	12.2	12.2	10.4	10.3	8.7	9.0	10.6	11.2	10.0	11.3	10.2	9.9	9.6	5.5	5.8	4.0	26-11	61-28	62-27	62-15	
8.1	8.4	9.0	9.7	6.7	6.1	10.9	10.9	9.3	9.4	8.9	8.8	9.9	10.9	9.6	10.7	10.2	9.5	9.0	5.0	5.9	4.0	26-11	61-28	62-27	62-15	
11.2	10.2	10.3	10.7	9.2	8.8	13.7	13.7	11.8	11.5	10.7	10.8	12.1	12.4	12.4	12.4	12.4	12.4	12.4	8.0	7.9	9.0	9.6	46-27	56-26	56-14	
11.6	11.6	11.9	12.6	10.2	9.8	15.2	15.2	13.5	12.5	11.7	12.5	14.1	13.2	13.8	12.8	12.4	12.5	9.1	8.6	9.8	9.6	8.8	6.6	44-17	50-17	
10.0	8.7	9.2	10.8	7.8	7.1	12.9	12.9	11.9	10.9	10.5	10.7	12.7	11.8	11.8	12.7	12.2	10.1	10.6	7.2	7.0	7.3	8.3	7.5	8.0	8.0	

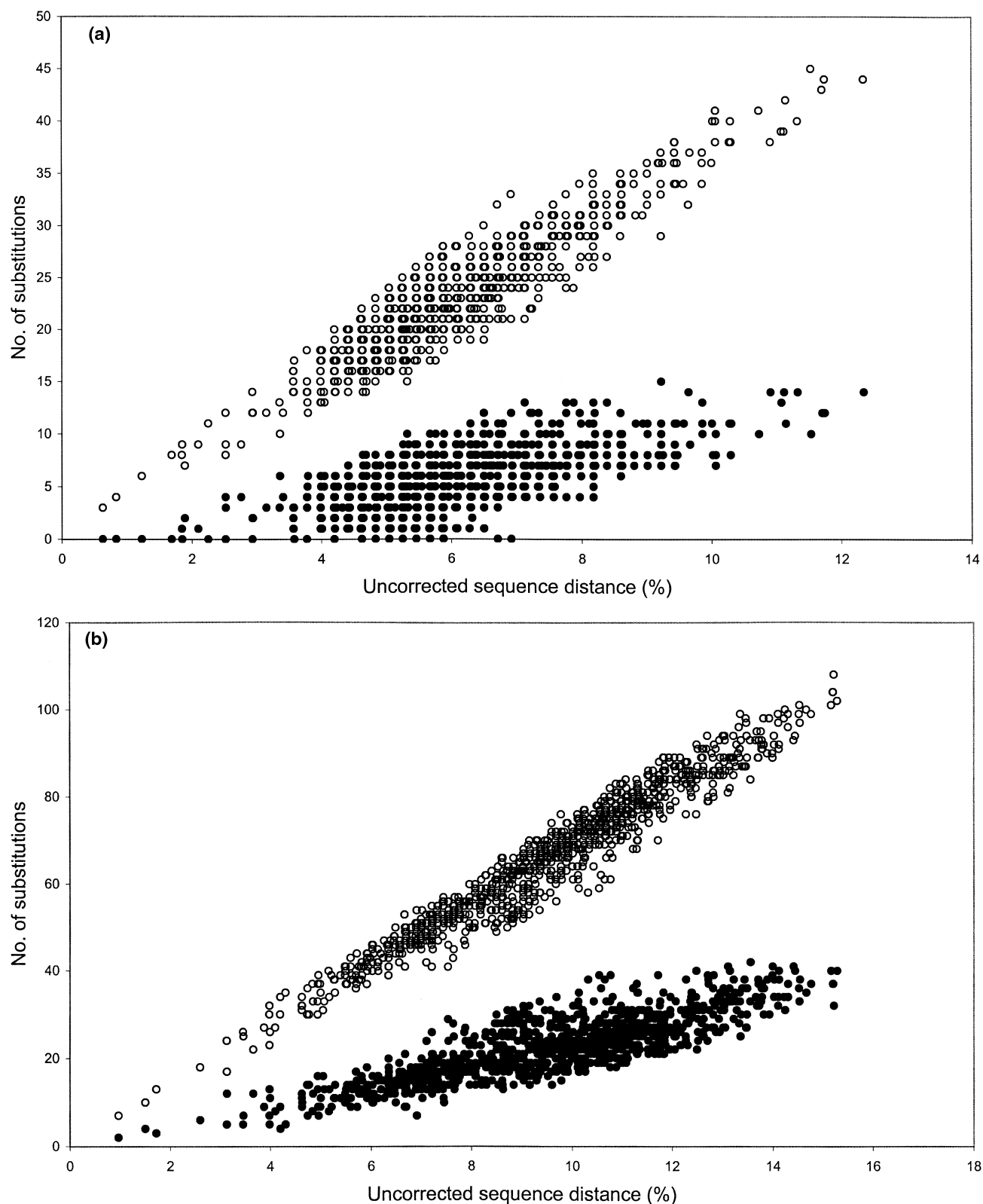


Fig. 2. Saturation plots for the *c-myc* (a) and RAG-1 (b) genes. The number of transitions (open circles) and transversions (closed circles) of each pairwise comparison of taxa plotted against the pairwise uncorrected sequence divergence

The only additional clade recovered in the strict consensus, is the sister-group relationship between the Trochilidae and the Apodidae/Hemiprocnidae-clade indicating monophyly of the Apodiformes.

The analysis of the combined data set yielded eight trees 2061 steps long (CI 0.34, RI 0.51). The strict consensus tree (Fig. 6) contains all the clades that received jackknife support in the analyses of the individual genes. In addition, the

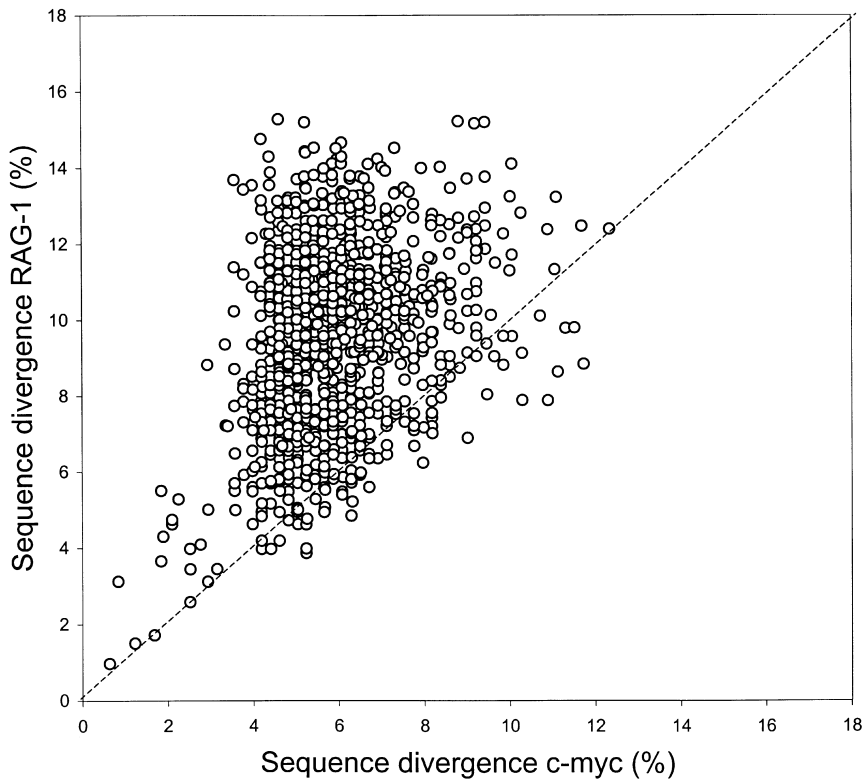


Fig. 3. Percentage sequence divergence of pairwise comparisons for RAG-1 plotted against uncorrected *c-myc* distances. Most data points fall above the dashed line that indicates a 1 : 1 ratio between the two genes, suggesting a faster mutation rate of RAG-1

Apodiformes now gains some jackknife support (59%) as does a sister-group relationship between the Galbulidae and Bucconidae (72%). The jackknife support values calculated from the combined data set are in most cases higher than those for the individual genes (cf. Figures 4, 5 and 6).

Discussion

Apodiformes

The sister-group relationship between the Apodidae and Hemiprocnidae is highly supported (100%) by the present analysis (Fig. 6). This relationship has long been recognized and the group is often referred to as the Apodi. The strict consensus of the combined analysis furthermore supports the monophyly of Apodiformes (59% jackknife support). Although a monophyletic Apodiformes was not obtained in the analysis of the *c-myc* gene (Fig. 4), all representatives of the Apodidae, Hemiprocnidae and Trochilidae share an insertion of four amino acids in this gene. Indels are very rare in this portion of the *c-myc* gene: only three additional occurrences of indels (nonhomologous to the one reported on herein) have been observed among the 175 species (representing 110 avian families) studied to date (Ericson et al. 2000). We believe the rarity of indels adds considerable strength to the hypothesis of monophyly of the Apodiformes suggested by the combined data set.

The Trochilidae and Apodi have been associated in many classifications, primarily based on myological and osteological similarities of the wing. Cohn (1968) have argued that these similarities are convergent due to a highly developed upstroke of the wing, and this has raised some doubts about the relationship between the two groups (Cohn 1968; Zusi and Bentz 1984). However, despite this, the monophyly of the group has been suggested by, for example, Burton (1971),

Cracraft (1981, 1988). Biochemical support for a monophyletic Apodiformes has also been suggested by the shared, unique electrophoretic pattern of the malate dehydrogenase (Kitto and Wilson 1966), by two independent studies of DNA-DNA hybridization data (Sibley and Ahlquist 1990; Bleiweiss et al. 1994), and is also supported by the present analysis (Fig. 6).

Caprimulgiformes

The Caprimulgiformes are generally considered to be monophyletic, 'although very little evidence has been offered in support' (Cracraft 1988). The present study includes representatives of four families traditionally referred to this order. Their monophyly was not corroborated in the analyses of the nuclear DNA data. On the other hand, as evident from the strict consensus tree (Fig. 6) the data are rather inconclusive and it remains to be determined whether the Caprimulgiformes actually is paraphyletic. In the *c-myc* gene tree all caprimulgiform taxa except *Nyctibius* are associated with Apodidae and Hemiprocnidae, in a clade which also includes the Bucerotidae (Fig. 6). This clade is not very robust, however, receiving no jackknife support, except the branch leading to Apodi. Furthermore, this clade is not present in the strict consensus tree based on the analysis of the combined data set (Fig. 6).

An association between the Caprimulgiformes and Apodiformes has been inferred from morphological studies (Cracraft 1981, 1988; Olson 1985). DNA-DNA hybridization data, however, suggest the Caprimulgiformes to be closer related to the Strigiformes, and that these in turn are the sister-group to the Apodiformes (Sibley and Ahlquist 1990). Although the data from the *c-myc* gene points at a possible relationship between Caprimulgiformes and Apodi, the result from the combined analysis is inconclusive.

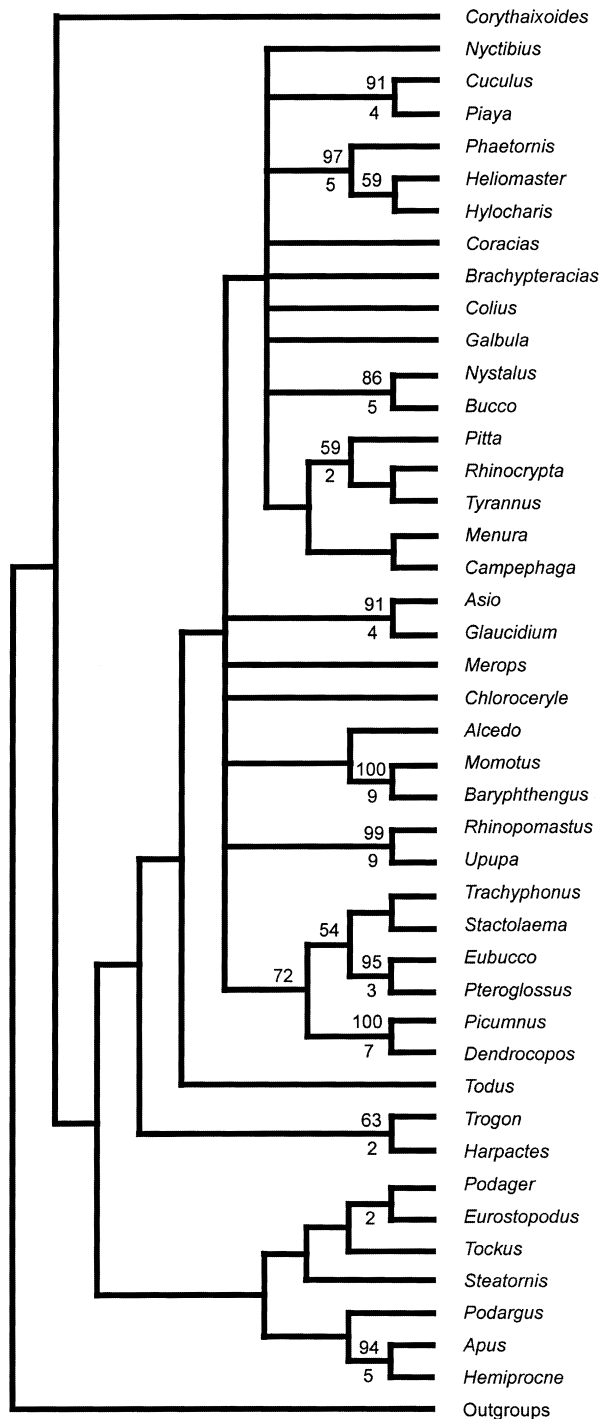


Fig. 4. The strict consensus of five most parsimonious trees obtained from the analysis of the *c-myc* gene (508 steps, CI = 0.3110, RI = 0.5368, RC = 0.2114). Parsimony jackknife support for the clades are indicated above the node, and Bremer support values below

Piciformes

The Piciformes *sensu* Wetmore (1960) consists of the families Galbulidae, Bucconidae, Indicatoridae, Ramphastidae Capitonidae and Picidae. Although the monophyly of the Piciformes has been disputed (Sibley and Ahlquist 1972, 1990; Olson 1983, 1985; Burton 1984), it is commonly agreed the families fall into two natural groups; the Galbulae (Galbulidae and Bucconidae) and Pici (the remaining families). Both these groups are

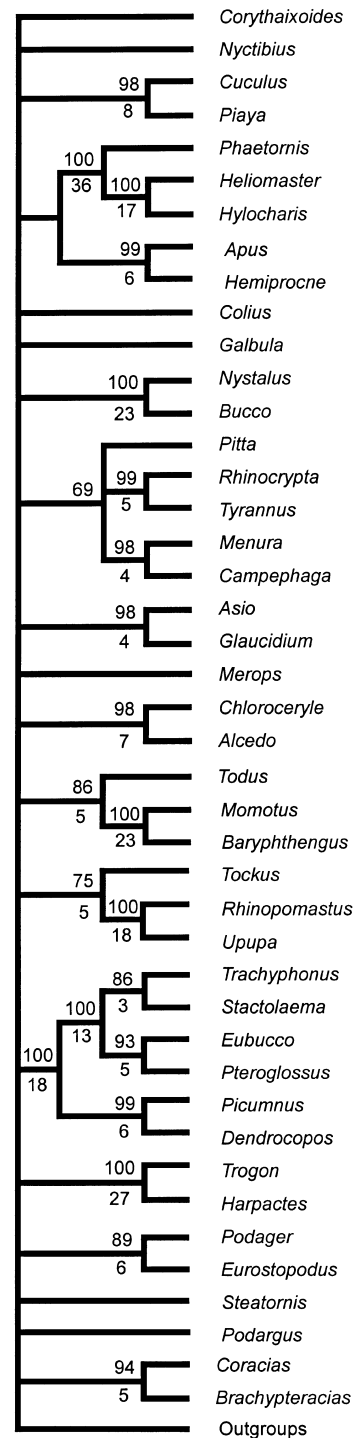


Fig. 5. The strict consensus of 87 most parsimonious trees obtained from the analysis of the RAG-1 gene (1520 steps, CI = 0.3641, RI = 0.5240, RC = 0.2127). Parsimony jackknife support for the clades are indicated above the node, and Bremer support values below

supported by several morphological synapomorphies (Swierczewski and Raikow 1981; Simpson and Cracraft 1981; Burton 1984). Also DNA-DNA hybridization data recognize these groupings (Sibley and Ahlquist 1990). Members of both Galbulae and Pici are characterized by a zygodactyl foot with a Type VI arrangement of the deep flexor tendons, i.e. the hallux (digit I), and the digits II and IV, are supplied by *M. flexor hallucis longus*, whereas *M. flexor digitorum* only supplies the

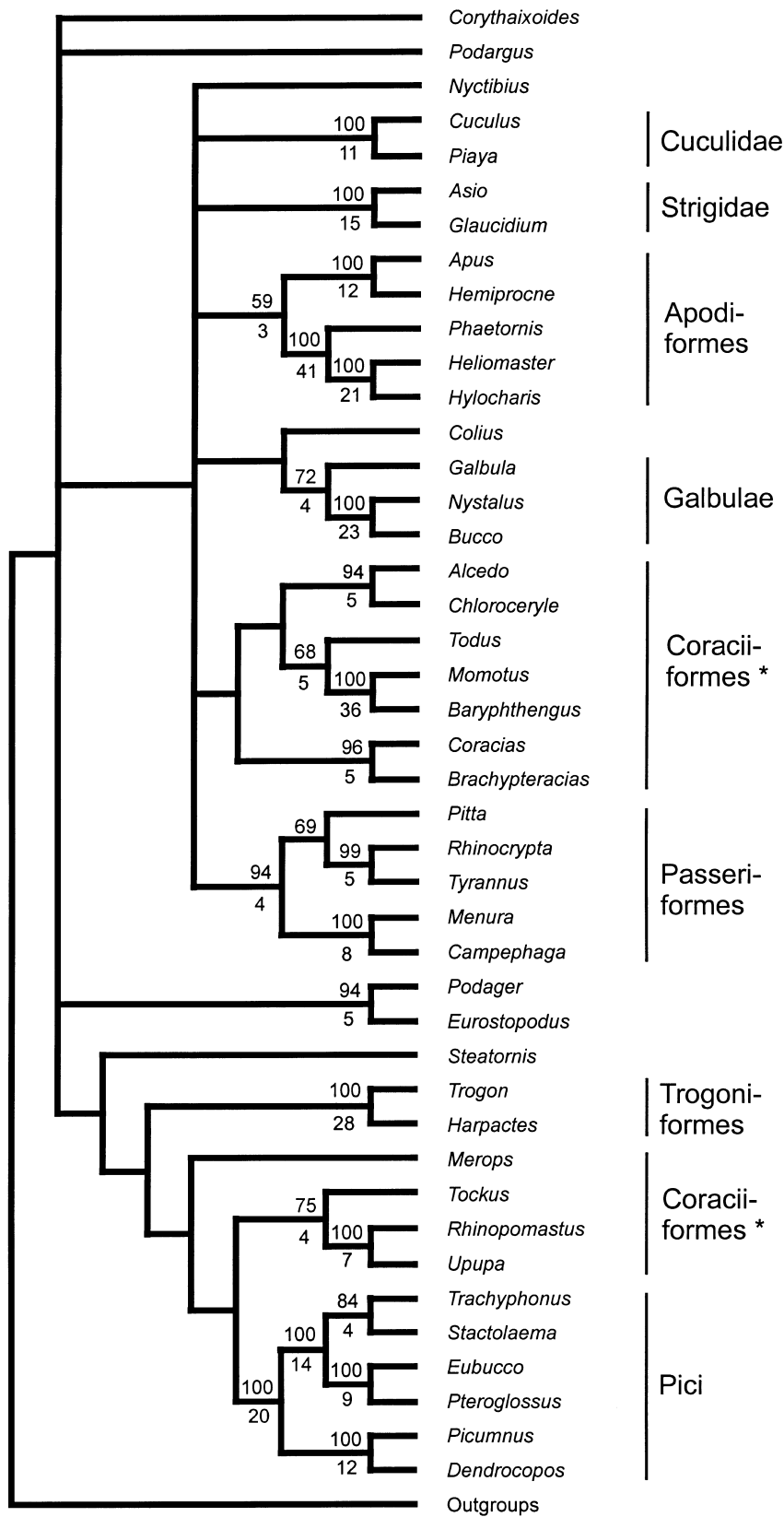


Fig. 6. The strict consensus of eight most parsimonious trees obtained from the analysis of the combined data set (2061 steps, CI = 0.3453, RI = 0.5144, RC = 0.2039). Parsimony jackknife support for the clades are indicated above the node, and Bremer support values below. Traditionally used taxonomic names for higher-level groups mentioned in the text are indicated. Asterisk for indicate the nonmonophyly of the Coracii-formes in the current analysis

digit III. In the other zygodactyl birds (Psittaciformes and Cuculidae), *M. flexor hallucis longus* supplies only digit I, and the *M. flexor digitorum* supplies digits II, III and IV. The zygodactyl foot with the Type VI arrangement is unique among birds and has been proposed as a synapomorphy for the

Piciformes (Swierczewski and Raikow 1981; Simpson and Cracraft 1981; Raikow and Cracraft 1983). Furthermore, in the Galbulae and Pici the *M. flexor hallucis* originates by three heads on the femur and fibula, whereas in most other birds it has one or two heads only (Raikow and Cracraft 1983).

Several studies, however, suggest the Piciformes (*sensu* Wetmore 1960) to be paraphyletic. On the basis of studies on the feeding apparatus, Burton (1984) suggested that the Galbulae should be placed in the Coraciiformes as the sister-group to a clade including the Coraciidae, Brachypteraciidae and Leptosomatidae. Sibley and Ahlquist (1972, 1990) also suggested a coraciiform affinity of the Galbulae based on similarities in the electrophoretic pattern of the egg-white proteins and DNA-DNA hybridization studies. In the latter study, the Pici was placed as the sister-group to most other neognathous birds besides Anseriformes and Galliformes. In other studies Pici has been associated with the Passeriformes (Olson 1983; Brom 1990; Mayr 1998).

Our study supports monophyly of the Pici within which a clade with the two woodpeckers (*Dendrocopos* and *Picumnus*) forms the sister-group to a clade consisting of the Ramphastidae and Capitonidae. Within the latter clade the Ramphastidae and the South American representatives of the Capitonidae group together, with the African capitonids as their sister-group. Paraphyly of the Capitonidae has previously been suggested both from morphological (Burton 1984; Prum 1988) and molecular studies (Sibley and Ahlquist 1990; Lanyon and Hall 1994). Galbulae, the second major clade of piciform birds, is also corroborated by the present analysis (Fig. 6). However, our data are unable to resolve the relationship between Galbulae and Pici.

Coraciiformes

Wetmore (1960) included in the order Coraciiformes the families Alcedinidae, Todidae, Momotidae, Meropidae, Coraciidae, Brachypteraciidae, Leptosomatidae, Upupidae, Phoeniculidae and Bucerotidae. The taxonomic delimitation of this order is, however, disputed. For example, Feduccia (1975a) and Maurer and Raikow (1981) included Trogoniformes in the group, whereas Burton (1984) suggested the Galbulae to be nested within the Coraciiformes. Furthermore, Burton (1984) and Olson (1985) have suggested the Upupidae, Phoeniculidae and Bucerotidae is a monophyletic assemblage closer to Pici than to the Coraciiformes.

Although the monophyly of the Coraciiformes is questioned some subclades may be recognized. A clade consisting of the Upupidae, Phoeniculidae and Bucerotidae have been suggested from both morphology (e.g. Burton 1984; Mayr 1998) and biochemical data (Sibley and Ahlquist 1990). Within this group evidence for monophyly of the Upupidae and Phoeniculidae comes from their possession of a uniquely derived stape (Feduccia 1975a, b) as well as several myological (Maurer and Raikow 1981) and osteological (Mayr 1998) characters. Although supporting such a sister-group relationship between the Upupidae & Phoeniculidae, Maurer and Raikow (1981) did not find them to be closely related to the Bucerotidae.

The present study supports the sister-group relationship between the Upupidae and Phoeniculidae, and that these in turn form the sister-group of the Bucerotidae (Fig. 6). Furthermore, the data indicates that this group is the sister-group to the representatives of the Capitonidae, Ramphastidae and Picidae, i.e. the Pici. This latter association does not receive any jackknife support. However, Burton (1984) and Olson (1985) have tentatively suggested a possible relationship between these groups.

Support is found for a sister-group relationship between the Momotidae and Todidae (Fig. 6), a clade also supported by

myology (Maurer and Raikow 1981), paleontology (Olson 1976) osteology (Mayr 1998), and mitochondrial sequence data (Espinosa de los Monteros 2000). Analyses of stape morphology (Feduccia 1975a) and myology (Maurer and Raikow 1981) suggest the Momotidae and Todidae to be part of a monophyletic clade consisting also of the Alcedinidae, Meropidae and Trogonidae. A similar association was suggested by Mayr (1998) but with the possible exclusion of Trogonidae. The present analysis of nuclear DNA data does not support this arrangement. Although the Alcedinidae is the sister-group of Momotidae and Todidae in the strict consensus tree, the Meropidae and Trogonidae were not found to be closely related to this clade but in the strict consensus tree they were placed near the Bucerotidae, Upupidae, Phoeniculidae and representatives of the Pici (Fig. 6).

Among the other taxa traditionally considered to be part of Coraciiformes, data support the sister-group relationship between Coraciidae and Brachypteraciidae, but the affinity of this group to other birds is not resolved. None of the other relationships involving coraciiform taxa suggested by the analyses of the individual genes (Figs 5 and 6), received any jackknife support.

Coliidae

The phylogenetic position of the Coliidae is very uncertain (see review in Sibley and Ahlquist 1990). The nuclear data in this study (Fig. 6) indicates a possible connection with Galbulae, although this association is not supported by the jackknife analysis.

Passeriformes

Based on both morphological and biochemical data (Raikow 1982; Sibley and Ahlquist 1990) the Passeriformes is regarded to be a monophyletic taxon that has evolved rather late compared to many other lineages of extant birds. Analyses of mitochondrial sequence data have arrived at the different conclusion that the Passeriformes is paraphyletic and that its phylogenetic position is basal to, e.g. the paleognathous birds and Galloanserae (Mindell et al. 1997, 1999; Härlid 1999). These hypotheses are not corroborated by the present analysis, and the nuclear data support the monophyly of the Passeriformes (Fig. 6). The relationships among the passerine birds included here furthermore agree with those found in a taxonomically more inclusive study by Irestedt et al. (in press).

Cuculiformes

The Cuculidae and the Musophagidae both possess an ambiens muscle and are not included in Anomalognatae *sensu* Beddard (1898). They have often been regarded closely related and placed in an order of their own, the Cuculiformes. Support for this arrangement comes from the observation that electrophoretic patterns of egg-white proteins of the Musophagidae are more similar to some cuculids than to any other birds (Sibley and Ahlquist 1972). However, results from analyses of DNA-DNA hybridization data contradict this association (Sibley and Ahlquist 1990). Instead, the Cuculidae was thought to be the sister-group to a large assemblage of birds consisting of 'more than half of the groups of living birds' (op. cit. p.370), including the Musophagidae. Mitochondrial DNA sequence data suggested the Cuculidae to be nested within the Anomalognatae (Espinosa de los Monteros 2000).

The two cuckoos *Cuculus* (Cuculinae) and *Piaya* (Coccyzinae) grouped together in all analyses of the present study, indicating monophyly of the Cuculidae, but monophyly of the Cuculiformes (Cuculidae and Musophagidae) was not corroborated by the analysis. In the strict consensus of the *c-myc* gene tree *Corythaixoides* (Musophagidae) is positioned basal relative to all ingroup taxa (Fig. 6). The Cuculidae, however, is placed more apical in the tree. Neither the RAG-1 gene tree nor the combined tree are conclusive regarding the relationships of the Cuculidae and Musophagidae.

Concluding remarks

The phylogenies obtained from the *c-myc* and RAG-1 genes are generally similar, although partly unresolved. Branches receiving high jackknife and Bremer supports in one gene tree are not contradicted by supported clades in the other gene tree. Conflicts have only been observed among clades with no support in the trees derived from the different data sets.

To a large extent, the basal relationship within the 'higher land birds' are unresolved in the present analysis. Phylogenetic relationships at higher taxonomic levels in birds have proven difficult to determine regardless of what kind of data is analyzed. The problem might be attributed to the combination of the great antiquity of many lineages, some having evolved in the early Tertiary or even earlier, together with the occurrence of periods in the avian evolution with rapid cladogenesis. As a result, phylogenetic trees with long-terminal branches and relatively short internodes are commonly found in analyses of higher-level relationships in birds (e.g. Espinosa de los Monteros 2000; van Tuinen et al. 2000) which in turn may lead to poorly resolved trees. Sequencing of multiple genes with different mutational rates together with a denser taxon sampling may improve resolution in the tree, but with a rapid, ancient diversification of the taxa the true phylogenetic pattern may also be difficult to detect regardless of the amount of data.

Acknowledgements

We wish to thank Peter Arctander, Jon Fjeldså and Jaime Garcia-Moreno (Zoological Museum, Copenhagen), Frederick H. Sheldon and Donna L. Dittmann (Museum of Natural Science, Louisiana State University), David Agro and Leo Joseph (Academy of Natural Science of Philadelphia), Joris Komen (National Museum of Namibia), Shannon Hackett, Thomas S. Schulenberg and David E. Willard (Field Museum of Natural History) and Susie Dunham for providing tissue. We are also thankful to Maria Arvidsson and Pia Eldenäs who have been of invaluable help in the laboratory and to Steve Farris and Mari Källersjö who ran the jackknifing analysis for us. Thanks also to Walter Bock, Joel Cracraft, Mari Källersjö, Gerald Mayr, and an anonymous reviewer for comments on earlier versions of this paper. This work has been funded by the Magnus Bergvalls Stiftelse, Olle and Signhild Engkvists Stiftelser, the Swedish Natural Science Research Council (grant no. B-AA/BU 01913–304), and the Swedish Museum of Natural History.

Zusammenfassung

Die von nuklearen DNA-Sequenzen abgeleiteten Kladen bei den 'Höheren and vögeln'

Es wurde eine Studie über die phylogenetischen Beziehungen bei den 'höheren Landvögeln' mit Hilfe einer Parsimonie-Analyse von DNA-Kernsequenzen zweier proteincodierender Genen, *c-myc* und RAG-1, durchgeführt. Kerngene wurden bisher noch nicht für die Untersuchung dieser phylogenetischen Frage eingesetzt. Die Ergebnisse

unterstützen mit hohen Jackknife-Werten eine Monophylie der Apodiformes (einschließlich der Trochilidae). Eine solche Einordnung wird auch durch die Beobachtung einer Einfügung von vier Aminosäuren im *c-myc*-Gen bei allen apodiformen Taxa unterstützt. Eine Monophylie konnte ebenso für die beiden picidiformen Gruppen, Glabulæ und Pici, bestätigt werden. Bei den Pici erweisen sich die Capitonidae als paraphyletisch, wobei die Bartvögel der Neuen Welt näher mit den Ramphistidae verwandt sind als mit den Bartvögeln der Alten Welt. Eine weitere Klade, die durch hohe Jackknife-Werte unterstützt wird, besteht aus den Upupidae, Phoeniculidae und Bucerotidae. Die Familien Momotidae und Todidae bzw. Coraciidae und Brachypteraciidae bilden ebenfalls gut unterstützte Kladen. Über die Monophylie der Ordnungen Coraciiformes und Piciformes können die Ergebnisse jedoch keine Entscheidung herbeiführen.

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